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Mangal communities of the "Salgado Paraense": Ecological heterogeneity along the Bragança peninsula assessed through soil and leaf analyses*

by

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Abstract

Mangroves in the Bragança peninsula occur in a variety of environmental settings differing in tidal influence and fresh water run-off. The construction of a paved road running through the middle of the peninsula modified the transversal flow of water. Five sites were sampled along this road: I. Coastal site near the village of Ajuruteua, II. Tidal creeks flowing into the lower Caeté river, III. Central lagoons, IV. *Avicennia* basin forest, and V. Upper Caeté estuary near the village of Acarajó. All but site III, harbored the three common mangroves species *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia germinans*. Monospecific communities of shrub-like *Avicennia germinans* stands characterized site III. Soils were highly organic therefore bulk density was inversely correlated to the concentrations of C and N. Sites I and V had the lowest salinity values. The highest salinity was measured in the *Avicennia* dominated sites III and IV. Nitrogen showed similar values in all sites, but S was clearly more abundant in sites II and V.

*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

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Leaf dimensions varied significantly between sites. Considering leaf area expansion as indicator of stress and $\delta^{13}C$ values as indicator of water use efficiency, site V was more favorable for *Rhizophora* and *Laguncularia* while site IV was so for *Avicennia*. Leaf shape measured as the length/width ratio was more variable in *Avicennia* and least variable in *Rhizophora*. Leaf nutrients were not correlated with soil nutrient content. Sodium and Mg were more concentrated in *Avicennia* leaves while Fe was more concentrated in *Laguncularia* and Mn in *Rhizophora* leaves. *Avicennia* showed the highest N and the lowest Ca concentrations as expected for being a glycinbetaine accumulator and an oxalate-former. $\delta^{15}N$ values indicate that N source for mangroves is essentially the mineralization of organic matter.

Keywords: **Brazil, Amazonia, mangroves, salinity, nutrients, leaf dimensions, stable isotopes.**

Resumo

Os manguezais da península bragantina occorem numa variedade de condições ambientais variando na inundação e no transcurso da água doce. A construção de uma estrada asfaltada atravessando a península modificou o curso da água transversal. Ao longo da estrada foram amostradas cinco áreas: I. Área costeira perto da Vila de Ajuruteua, II. Furos vazando nas baixas do rio Caeté, III. Lagoas centrais, IV. Bosque de bacia de *Avicennia* e V. o Estuário do rio Caeté perto da Vila de Acarajó. Todas essas áreas menos a área III são habitadas pelas três espécies comuns de mangue *Rhizophora mangle*, *Avicennia germinans* e *Laguncularia racemosa*. A área III foi caracterizada por comunidades monoespecíficas de *Avicennia germinans* passando a forma arbustiva. Os solos eram altamente orgânicos pelo qual a densidade era correlacionada inversamente com as concentrações de C e N. As áreas I e V mostraram os menores valores de salinidade. A salinidade mais alta foi medida nas áreas dominadas por *Avicennia* III e IV. O nitrogênio mostrou valores similares em todas as áreas, mas S foi claramente mais abundante nas áreas II e V. A área folhar variou significativamente entre as áreas. Considerando a expanção da área folhar como indicador de "stress", e valores de $\delta^{13}C$ como indicador do uso eficaz de água, a área V foi mais favorável para *Rhizophora* e *Laguncularia* enquanto a área IV foi assim para *Avicennia*. A forma da folha medida através da relação de cumprimento/largura foi mais variada em *Avicennia* e menos variada em *Rhizophora*. Os nutrientes das folhas não foram correlacionados com o conteúdo de nutrientes do solo. Na e Mg eram mais concentradas nas folhas de *Avicennia* enquanto Fe era mais concentrado em *Laguncularia* e Mn em folhas de *Rhizophora*. *Avicennia* mostrou as concentrações mais elevadas de N e as concentrações mais baixas de Ca como foi esperado por ser um acumulador de glicinbetaina e um formador de oxalato. Os valores de $\delta^{15}N$ indicam que a fonte de N para manguezais é essencialmente a mineralicação de matéria orgânica.

Introduction

The Atlantic coast of northern Brazil from Orange Cape (Amapá state) in the north to the estuary of Maranhão in the south is lined by a thick band of mangroves that thrive under a high rainfall regime and abundant nutrient supply carried by large rivers. This region denominated as the Amazonian ecoregion by SULLIVAN SEALY & BUSTAMANTE (1999) includes a variety of coastal environments differentiated by the influence of the plume of the Amazonas River. The coastal plain located east of the Marajó bay in the Amazonas delta, between the mouth of the Tocantins-Pará rivers and the estuary of Maranhão is a submersion coast "deeply dissected by many wide-mouthed estuaries that penetrate inland for several km" (SCHAEFFER-NOVELLI et al. 1990; FRANZINELLI 1992). Its rainfall regime is relatively humid towards the Belem area with a well-defined dry season lasting 1-3 months and semihumid in the Maranhão estuary with a dry season lasting 5 months in average (IBGE, Diagnóstico Brasil 1990). This area receives large fresh water inputs from rivers such as the Pará-Tocantins (towards Belem area), Gurupí, Maracacumé, Turiaçu, Pericumá, and Miarem (São Luis area). The fresh water and sediment plumes of these rivers are deflected towards the northwest by the North Equatorial oceanic current (NITTROUER et al. 1995). This geomorphological and climatic setting generates a pattern of vegetation varying in composition, structure, and productivity according to soil factors (nutrition and texture), hydrology (fresh water availability), and tidal effects along the coast and rivers (salinity and flooding). Mangrove communities in this area are constituted mainly by three species, *Rhizophora mangle* L., *Laguncularia racemosa* (L.) GAERTN. F., and *Avicennia germinans* (L.) STEARN. (designated in the rest of the paper only by their genus name) that occur under similar climate, but different levels of fresh water run-off, and tidal influences. This provides an opportunity for a detailed study of site-plant nutritional and stress conditions through the analysis of structural development and nutritional composition of photosynthetic tissues.

This paper describes the results of a systematic sampling of leaves and soils in mangrove communities differing widely in composition and density in the peninsula of Bragança, Pará, Brazil. The objective was to characterize plants and soils on the basis of their nutrient content and soluble ion content determining salinity stress. These parameters are taken as indicators of ecological heterogeneity.

Description of the study area

The study area is the Bragança peninsula delimited by the Taperaçu and Caeté rivers (Fig. 1). This peninsula is crossed through its middle by a paved road leading from the city of Bragança to the coastal village of Ajuruteua. Along this road, we sampled mangrove communities in a variety of environments differing in their distance to the sea and their hydrologic, and presumably edaphic conditions. The salinity and ionic composition of the Caeté river varies along its way from Bragança to Ajuruteua, being low at the level of Bragança (~ 2-5 ‰) and moderate at the mouth in Ajuruteua (19-30 ‰). Salinity also fluctuates seasonally following the rainfall distribution (COHEN et al. 1998; MENEZES et al. 2000).

The construction of the road modified to a varying extent the natural drainage patterns, in some cases interrupting free water flow from one side to the other near the middle section of the peninsula. This disturbance apparently caused an extensive mortality of the mixed mangrove communities located to the northwestern side of the road between 12-15 km from the city of Bragança (CARVALHO 2000).

There are no meteorological data available for the area between Bragança and Ajuruteua. The nearest station is located in Tracuateua (01°05'S; 47°10'W), about 16 km from Bragança, with a rainfall recording period of 24 years. Rainfall averages 2482 mm per year, varying between 1300 and 4400 mm during the observation period. Rainfall is highly seasonal with rainfall above 200 mm per month from January to June, and less than 25 mm per month from September to November (Fig. 2).

Site I. Mangroves near the Atlantic coast (**Ajuruteua**)

The village of Ajuruteua is located near the broad mouth of the Caeté River. The mangroves at this site have low stature (<12 m), forming a narrow mixed mangrove fringe (<50 m wide) along a tidal creek, dominated by *Rhizophora* and *Avicennia* in the interior, and bordered with scattered *Laguncularia* shrubs and trees. The external border of the mangrove community interface with a salt grass community located on higher, sandy soils (*Sporobolus virginicus*), with frequent occurrence of the climber *Rhabdadenia biflora.*

Site II. Mangrove communities along tidal creeks ("furos") at the lower Caeté river **(Furo Grande and Furo Café)**

The furo Grande cross the peninsula from the Caeté to the Maiaú bays. The fringe at this site is constituted by a mixed forest (>20 m tall, >20 cm diameter at 1.5 m height, dbh) with predominance of *Rhizophora,* on a highly organic-clay substrate with strong H_2S odor when disturbed. The furo Café fringe is a mixed forest with arboreal *Laguncularia* (15-20 cm dbh), and few large sized *Avicennia* (dbh >20 cm). Both fringes are flooded daily by tides.

Site III. Central area of the peninsula, flooded by rain, sporadically influenced by high tides (**Dwarf *Avicennia***)

This site is characterized by a shrub-like monospecific *Avicennia* forest located at both sides of the road bordering large water ponds dominated by *Eleocharis mutata.* This area is visible in satellite images showing an extension of about 3.5 km in the E-W direction and about 1.5 km in the N-S direction (see Fig. 1). The *Avicennia* stands were up to 3 m tall, flooded by rainwater. The soil has a sandy-clay texture, coring it liberated a strong H_2S odor indicating the anoxic conditions of the subsoil, and the presence of reduced S probably of marine origin. We measured a tree density of 250 stems/ 0.1 ha with an average dbh of 4.1 cm. The occurrence of these dwarf *Avicennia* stands, apparently isolated from the main body of the fringe mangroves of the Caeté river, deserves special research to establish its origin and functional properties.

IV. ***Avicennia* forest**, on the upper basin of Pará tidal creek

At this site, a contrasting aspect of the vegetation at both sides of the road was evident. At the southeast side of the road there was a basin mangrove forest dominated by *Avicennia* with scattered individuals of *Rhizophora* and *Laguncularia.* Tree height was above 10 m with a density of 100 stems/0.1 ha and an average dbh of 11.6 cm. This forest constitutes the upper part of the mangrove fringe of the Pará tidal creek that leads into the Caeté River. The transect from the road to the fringe itself shows a clear zonation from nearly pure *Avicennia* forest to the *Rhizophora* forest at the fringe (MENEZES 2000). CARVALHO (2000) described this forest as a mixture of *Rhizophora* and *Avicennia* (47 and 38% respectively), and reported the presence of *A. schaueriana* as a minor component in several plots.

At the northwest side of the road there was a large area, visible from satellite images (G. KRAUSE pers. comm.), a degraded area showing extensive mangrove mortality, mostly of *Avicennia*. This area appears flooded by rain during the rainy season. It seems that it has been cut off from its natural drainage from the Pará creek. It has been hypothesized that the large seasonal variations in salinity caused by lack of flooding and water impounding may have caused the extensive mangrove mortality. This area is presently very heterogeneous, with large (>15 cm dbh) dead *Avicennia* trees, and patches of dead shrubby *Laguncularia*. In some places, new establishment of *Avicennia* and *Laguncularia* was observed. These species were described as vigorous pioneers in the degraded area by CARVALHO (2000).

V. Fringe mangroves of the upper Caeté River near the village of Acarajó (**Acarajó**)
In this area a fringe with large (>20 m tall, >20 cm dbh) *Rhizophora* and *Avicennia* trees were sampled. Patches of smaller *Laguncularia* were observed at the landwards border of the site. Tree density measured in this site was 90/0.1 ha with an average dbh of 34 cm.

The vegetation has been frequently disturbed for the establishment of rice plants. To do that the *Rhizophora* dominated vegetation is felled and the soil is drained through a net of shallow channels. This action desalinates the upper soil layer so that rice plants can establish and grow.

Materials and methods

Leaves

Adult, healthy, fully exposed leaves of the mangrove species found at each site were collected (three trees, ten leaves per tree). The leaves without petioles were gently cleaned in the laboratory with moist tissue paper, and their shape was drawn on paper to measure leaf area, length, and width. Leaves were then dried in a ventilated oven at 90 ºC during 48 hours and weighed after cooling at room temperature. All leaves pooled per species and site were grounded for subsequent chemical analyses.

Soils

Soil samples were obtained at each site with a cylindrical 50 cm long, 8 cm wide soil corer. When possible, separate samples were taken from areas underneath each of the mangrove species found. Soil cores were subsampled from the upper 0-10 cm and the lower 40-50 cm to detect differences between soil layers determined by superficial water movement and organic matter deposition.

Soil samples were brought from the field in plastic bags for further processing. In the laboratory each sample was subsampled by filling 2 plastic cylinders (3 cm wide, 1.3 cm height = 9.2 cm^3). One subsample was put into a plastic bottle to which 50 cm^3 of factory processed drinking water were added. The mixture was homogenized with a glass stirrer and allowed to stand for 12 hours. The conductivity of the clear supernatant was measured with a Cole-Parmer conductivity meter with an Au-cell. The second subsample was air dried and weighed. The sample was stored for subsequent chemical analyses. The data obtained were used to calculate bulk density (air dry weight/volume) and specific soil conductance (conductance x 50/air dry weight).

Chemical analyses

Both leaf and soil samples were digested in a mixture of nitric acid-hydrogen peroxide and analyzed for P, Na, K, Ca, and Mg using ICP techniques (LUH HUANG & SCHULTE 1985). Carbon, nitrogen and sulfur were measured with a combustion technique in a LECO CNS analyser (TABATAI & BREMMER 1991). These analyses were performed at the International Institute of Tropical Forestry (USDA Forest Service, Río Piedras, Puerto Rico).

Natural abundance of Carbon 13 ($\delta^{13}C$) and Nitrogen 15 ($\delta^{15}N$) were measured in the laboratories of CENA, Piracicaba (University of São Paulo) using standard mass spectrometric techniques. Analysis of ^{13}C was intended to evaluate drought stress and water use efficiency (FARQUHAR et al. 1982; LIN &

STERNBERG 1992) while ^{15}N analysis was expected to indicate availability of mineral N in the soil (MARTINELLI et al.1992).

Results

1. Soil characterization

Sites differed markedly in most physico-chemical properties analyzed following a pattern according to their location along the Bragança-Ajuruteua road (Table 1). Bulk density varied from 1.6 g cm^{-3} in the coastal site to 0.6 g cm^{-3} in mangroves of the Furos Grande and Café. As these soils are highly organic, variations in bulk density were inversely related to the soil carbon and nitrogen concentrations (Fig. 3). Sites dominated by tall *Rhizophora* forest (sites II and V) and the shrub-like *Avicennia* site (III) showed the highest carbon concentrations in the upper 10 cm. The coastal site (I) had relatively low superficial carbon content in correspondence with the smaller structural development of the mangroves here. Also, site IV corresponding to the *Avicennia* basin and the dead-mangrove area, was relatively low in carbon. Nitrogen concentrations followed the same pattern as would be expected from the association of these two elements in the soil organic matter. Sulfur and carbon concentrations were positively correlated only in the upper 10 cm of soil.

Specific soil conductance is a measure of absolute salinity that eliminates variations resulting from changes in soil water content. If in a certain site the amount of soil per unit of soil weight or volume remains constant, the measured salinity with a salinometer is a function of the amount of liquid water present, and as such is submitted to strong diurnal and seasonal variations. The average specific soil conductance at 0-10 cm was lower than at 40-50 cm in all sites, probably reflecting the leaching effect of the rain during the collection period (Table 1). Both the Ajuruteua and Acarajo sites showed the lower soil concentrations both at superficial and deep soil layers. Interestingly, the sites III and IV had similar conductance values, in spite of having contrasting types of vegetation.

A correlation analysis was conducted on Table 1 to detect similarities among the factors analyzed. We considered as significant only linear correlations explaining 70% or more of the variance ($r^2 \geq 0.7$). As expected, C and N were highly correlated, because of their association in soil organic matter. The significant correlation found between the concentration of P and those of K and Mg is probably a consequence of the large organic matter input of the vegetation.

Specific soil conductance was determined largely by the concentration of Na (Fig. 4a). The other alkaline ions were also linearly correlated to specific soil conductance, but their importance was considerably lower (Fig. 4b). The relationship between Na and the other cations was not linear but logarithmic, showing that as the soil salinity increases the contribution of Na becomes more important.

To compare the rest of the measured soil elements independent of differences in bulk density we calculated the amount of elements per unit soil volume (mmol m^{-3}= element concentration mmol kg^{-1} x bulk density kg m^{-3}). The elements followed contrasting patterns (Fig. 5). Sulfur and Na contents were always larger in the deeper soil layer. However, while S content was larger in the tall mangrove sites (II and V), the contents of P, Mg, and Na were higher in the *Avicennia* sites (III and IV). Nitrogen content was similar at both depths in all sites, and Ca was always lower than K and Mg.

2. Leaf characterization

Size and shape

Leaf size and shape varied significantly among the sites sampled (Table 2). *Rhizophora* and *Laguncularia* produced larger (area) and heavier (weight) leaves in the low salinity site V. However, while specific leaf area (SLA) was also higher at this site for *Rhizophora*, the highest value of SLA for *Laguncularia* was found at site IV. *Avicennia* showed a contrasting behavior, producing larger leaves in site IV and heavier leaves in site II. Therefore its highest SLA was recorded in site IV, although it was not different from site V. The shrub-like *Avicennia* community of site III had significantly smaller and lighter leaves than all the other samples. The range of variation of leaf area (([minimum/maximum leaf area]-1)*100) was smaller in *Rhizophora* (26%), intermediate in *Laguncularia* (42%) and large in *Avicennia* (60%).

Leaf shape (ratio length/width) varied significantly in all sites, but the ranges were small in *Rhizophora* (0.2), intermediate in *Laguncularia* (0.5), and comparatively large in *Avicennia* (1.4).

Nutrient concentration

The leaf samples were lumped together per species and per site. Therefore, it is not possible to make statistical analyses of differences between nutrient concentrations among sites. However, these nutrient averages represent a large population of leaves and therefore the tendencies are indicative of species and site differences.

Ash concentration was directly correlated to the concentration of alkaline elements and silica. It was higher in *Avicennia*, followed by *Rhizophora* and *Laguncularia* (except site V) (Table 3). Concentrations of C and S varied little among sites and species, but N concentration were consistently higher in *Avicennia* and lower in *Laguncularia*. The C/N ratios, that are indicative of the quality of the organic matter for herbivores are smaller in *Avicennia* and similar for *Rhizophora* and *Laguncularia*. In contrast, the N/S ratio, that is a measure of the amount of S per unit leaf protein, was remarkably constant among sites and species.

The largest differences among sites and species were found within the components of the ash (Table 4). *Rhizophora* showed the lowest concentrations of P and Fe but the highest concentration of Mn. *Laguncularia* showed the lowest Na concentrations at each site (except site V) and had significantly higher concentrations of Fe. Lower Ca and higher Na concentrations characterized *Avicennia*. Therefore, at each site the Na/K and Mg/Ca ratios of this species were consistently higher than those of the other two.

Stable isotopes

Average of $\delta^{13}C$ and $\delta^{15}N$ did not differ statistically among species (Table 5). Variation range of $\delta^{13}C$ values was small in *Laguncularia* (0.60), intermediate in *Rhizophora* (1.96), and large in *Avicennia* (2.1). *Rhizophora* had more negative values in site V, indicating the lower salinity and possibly lower water stress at this site, while the sites I and IV showed values indicative of higher water use efficiency. By contrast, *Avicennia* had the most negative $\delta^{13}C$ value of all samples in site III. The lowest water use efficiency for *Avicennia* was recorded for site IV.

$\delta^{15}N$ values were larger for all species in site IV, and smaller for all species in site

V (Table 6). Their ranges were smaller for *Rhizophora* (1.4), intermediate for *Avicennia* (2.3) and larger for *Laguncularia* (4.7).

Discussion and conclusions

Heterogeneity of soils

Soils are in general highly organic as frequently found in areas submitted to tidal flooding (FASSBENDER 1984). Bulk density was negatively correlated with C and N concentration. The comparison of superficial and deep soil samples showed that alkaline elements and S were more concentrated in the deeper layer. It is possible that sampling at the end of the rainy season may have reduced salt concentration at the soil surface. This situation may change during the dry season, as soluble salts may be transported to the surface by capillary water, and then accumulated there as the water evaporates. Concentration values in the deeper soil is probably more constant throughout the year, and therefore may represent better the long term salinity and nutritional characteristics of these soils.

The sites differed significantly in specific conductance, and concentrations of all the elements analyzed. Sites near the oceanic coast and in the upper Caeté river (I and V) had lower conductance and contents of alkaline ions (Fig. 6). This similarity derives from different situations, in the first case tidal flooding was limited, while in the Acarajó site fresh-water run-off appeared to be the determining factor. The cultivation of rice during the rainy season in site V reinforces this hypothesis. Higher availability of fresh water run-off allows for an effective salt leaching from the superficial soil layers after mangroves felling and soil drainage.

Sodium content was markedly higher in the sites III and IV, located at greater distance from the river fringe or the coastline. We hypothesize that those two sites are the most stressful because salinity will increase dramatically during the dry season affecting vegetation development. The presence of a peculiar dwarf *Avicennia* forest in site III is probably associated with this environmental constrain. It would be worthwhile to investigate the dynamics of growth and photosynthesis of this community during contrasting seasons in the year. Another remarkable result is that the content of S in sites III and IV is much lower than that of *Rhizophora* dominated sites II and V.

Leaf size and chemical composition

Measured leaf characteristics varied significantly among sites (Table 2). The largest differences for leaf area were observed between sites IV and V for *Rhizophora*, between sites II and V for *Laguncularia* and between III and IV for *Avicennia*. However, *Rhizophora* was less variable while *Avicennia* varied the most, both in area and weight. Considering that leaf area is strongly modified by environmental stresses such as salinity, hypoxia or drought (LUGO et al. 1976; MEDINA & FRANCISCO 1997) we conclude that site V is least stressful for *Rhizophora* and *Laguncularia*, while site IV is least stressful for *Avicennia*. Site III deserves further research because it appears to be highly restrictive for structural development of *Avicennia*.

Variations in leaf shape (length/width, L/W) among sites followed the same pattern as leaf area. This factor is apparently associated with the accumulation of salt in the leaf tissue. Larger ratios in *Avicennia germinans* correspond to low salinity levels in leaf tissues (SUÁREZ 2000). In the present case, the larger L/W ratios in *Avicennia* and *Laguncularia* correspond to the lowest Na concentrations in leaf tissue.

Nutrient analyses of leaf tissues do not correlate directly with the total amounts measured in the soils. Sites II and IV were richer in S, but the plants did not show significant differences in their S concentrations. Nitrogen was homogeneously distributed in the different sites, but *Avicennia* had consistently higher N concentrations, probably because it uses glycinbetaine as a compatible solute for salt tolerance (POPP et al. 1984; MEDINA & FRANCISCO 1997). *Avicennia* also had consistently higher concentrations of Na in their leaves without clear correlation with soil Na concentration. This is also the case for total Ca in the leaves. *Avicennia* showed lower Ca concentrations, by a factor of 3, than the other species. *Avicennia* species have high oxalate concentrations in their cell sap (POPP 1984) causing a precipitation of Ca ions. Our results showing low concentrations of total Ca suggest that the presence of free oxalate at the root level possibly prevents its transportation in the xylem. One little reported fact is that *Laguncularia* in this area shows significantly higher concentrations of Fe while *Rhizophora* does the same with Mn. The physiological role of these relative accumulations is not clear.

The isotope analyses suggests that N sources for mangrove nutrition in this areas depends solely on the mineralization of organic N. Direct contribution of N_2-fixing organisms is unlikely. The positive values of $\delta^{15}N$ are indicative of an open N-cycling characterized by an abundant supply of nitrogen (MARTINELLI et al. 1999). The results on $\delta^{13}C$ reinforce the hypothesis that site III is the most stressful for *Avicennia*, and it is there where it shows it highest water use efficiency as measured by discrimination of carbon 13 (FARQUHAR et al. 1982; LIN & STERNBERG 1992; MEDINA & FRANCISCO 1997). As expected site V is the least stressful for *Rhizophora* and *Laguncularia* but not so for *Avicennia*. Both *Rhizophora* and *Laguncularia* have less negative $\delta^{13}C$ values in site IV, but *Avicennia* has there its more negative value.

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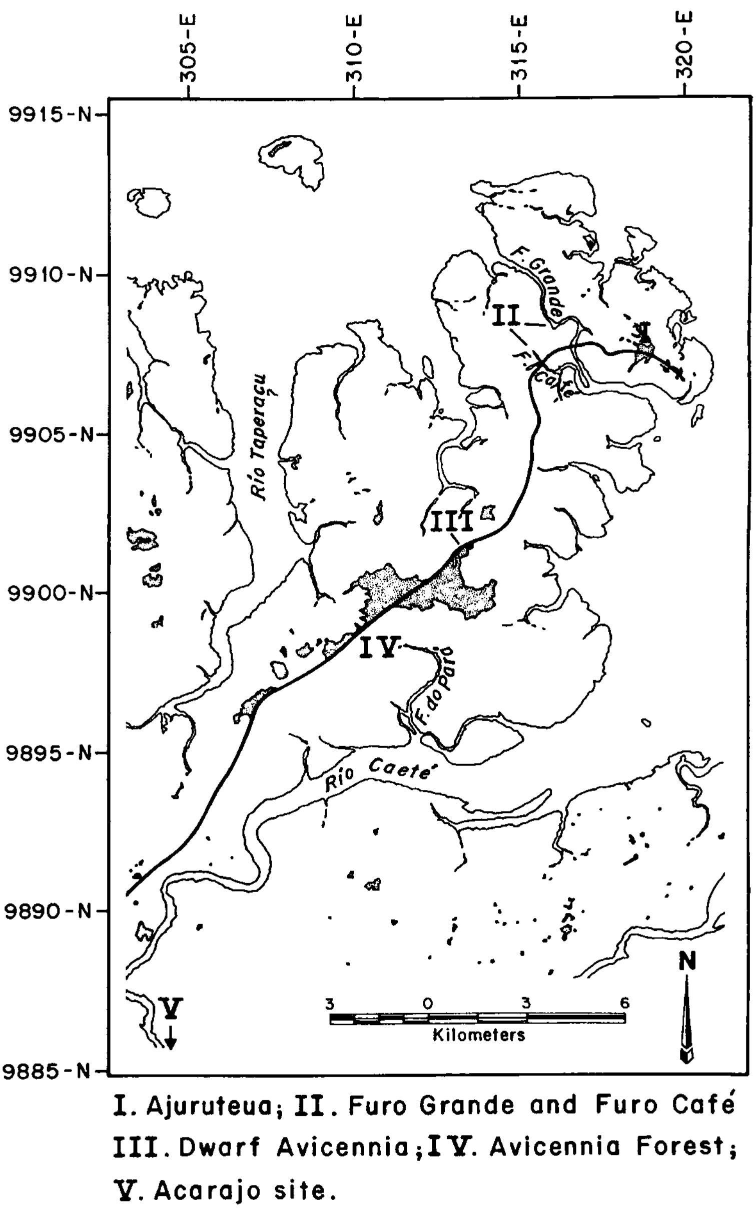

Fig. 1:
Location of the samplig sites along the road Bragança-Ajuruteua. The Acarajó site is outside of the map.This map was drawn from a georeferenced satellite image of the Brangança peninsula. The numbers on the border of the map correspond to UTM units (Universal Transverse Mercator) are given in meters from the reference grid and should be multiplied by 1000. The grid scale is therefore 5 km.

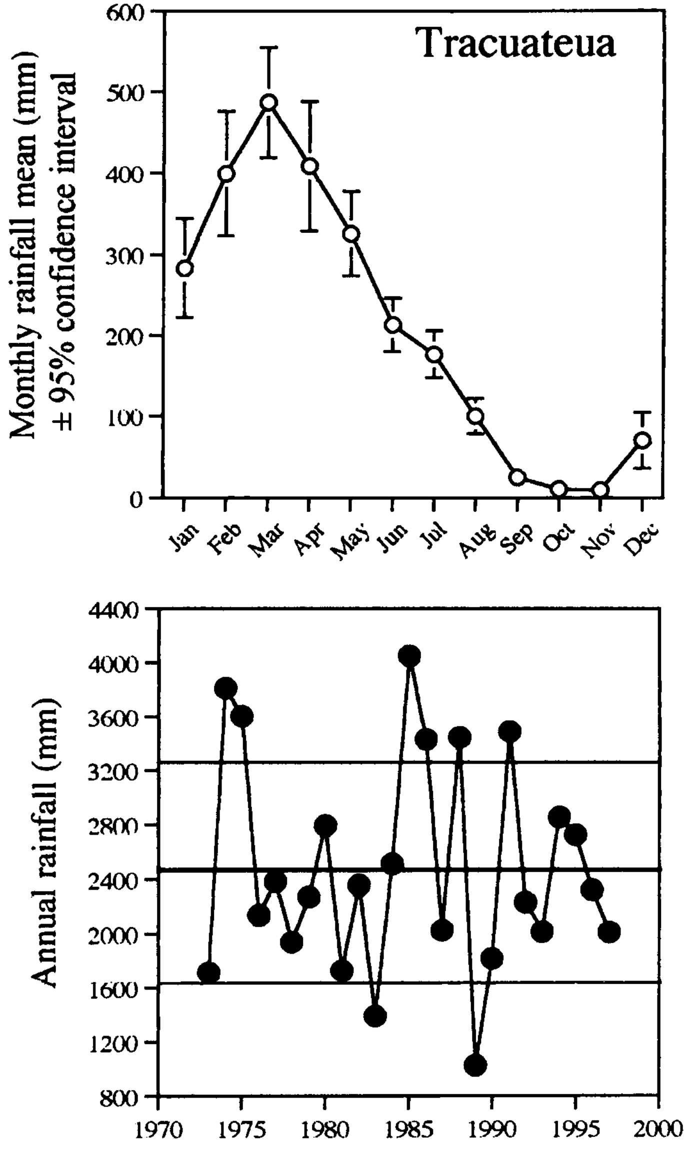

Fig. 2:
Upper panel: Average monthly rain distribution (± 95% confidence interval) for the station of Tracuateua located 16 km from Bragança. Lower panel: Interannual variation of total rainfall for the station of Tracuateua.

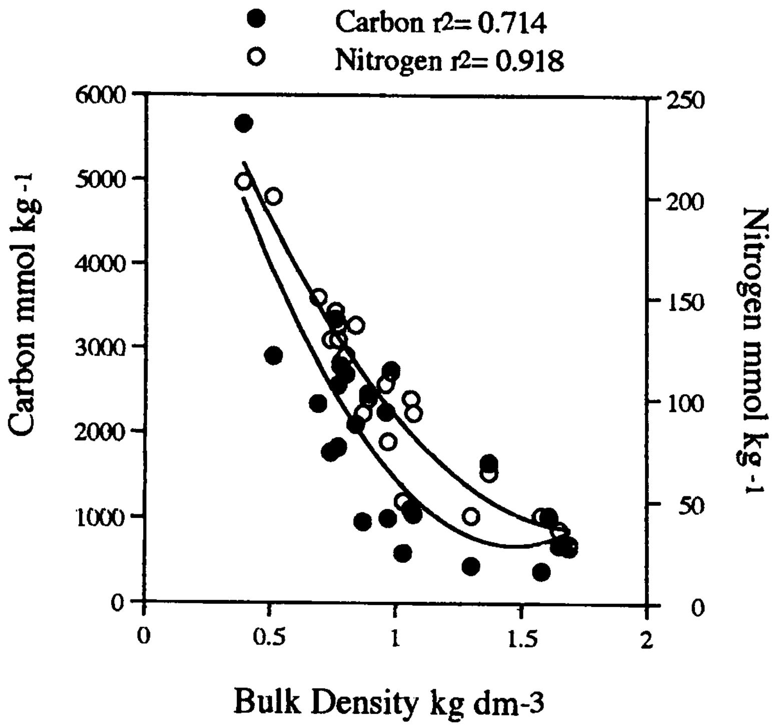

Fig. 3:
Relationship between Carbon and Nitrogen concentration and soil bulk density of soil samples taken from 0-10 and 40-50 cm depth.

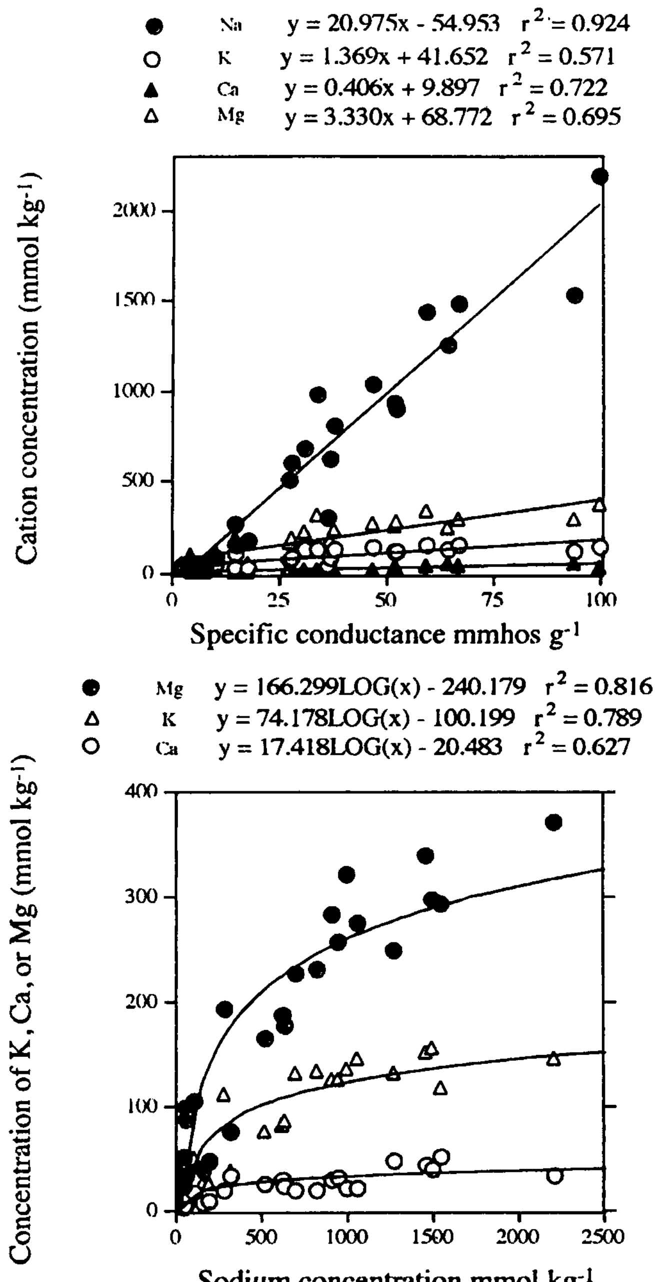

Fig. 4:
Upper panel: Relationship between soil specific conductance on a dry weight basis and the concentration of cations measured in the same sample. Lower panel: Relationship bewteen Na concentration and concentration of other cations showing that salinity increase determined essentially by Na concentration is not followed linearly by the concentration of other cations.

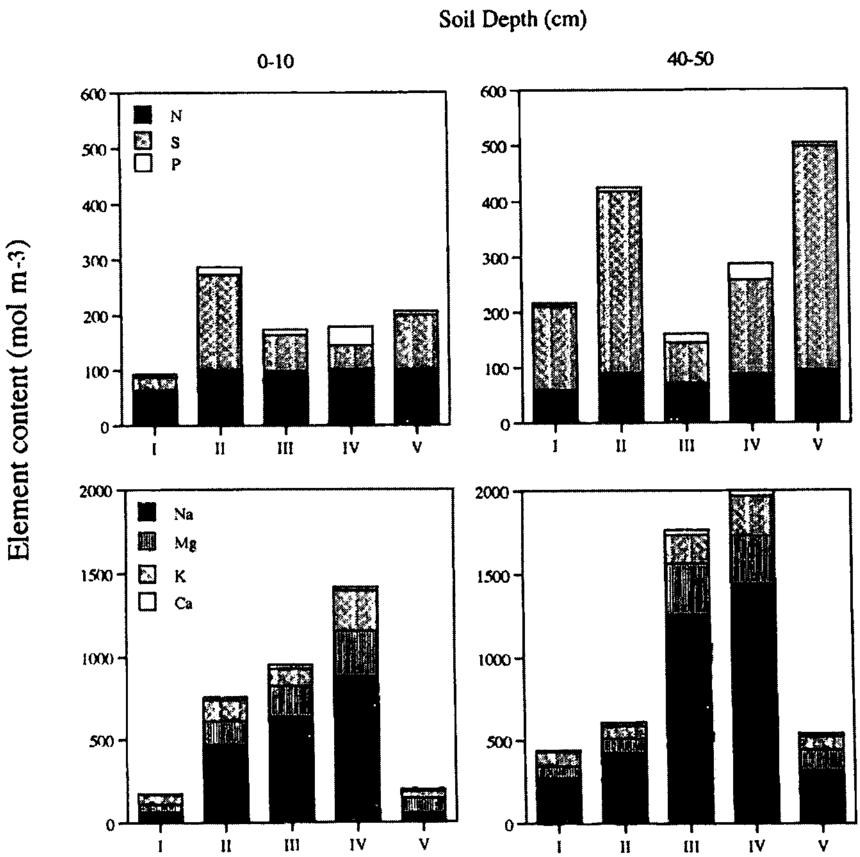

Fig. 5:
Distribution of nutrients associated to organic matter (N,S and P) and cations at different soil depths.

Table 1: Collection sites and physico-chemical characterization of soil samples.

Collection site	Depth cm	Habitat	Bulk Density g cm^{-3}	Specific Conductance mmhos g^{-1}	C	N	S	P	K	Ca	Mg	Na
					mmol kg^{-1}							
(I) Ajuruteua	(0-10)	*Rhizophora*	1.65	7.5	683	36	15	2.2	21	5	34	46
		Avicennia	1.58	4.4	383	43	13	1.4	15	4	23	33
	(40-50)	*Rhizophora*	1.61	17.3	1017	43	98	2.0	25	9	47	179
		Avicennia	1.69	14.3	658	29	86	1.8	25	7	40	153
(II) Furos of lower Caeté	(0-10)	Furo Grande, *Rhizophora*	0.77	36.4	2558	129	262	8.9	85	24	177	625
		Furo Café, *Laguncularia*	0.51	51.7	2900	200	280	14.9	126	30	283	901
	(40-50)	Furo Grande	0.80	35.7	2683	121	480	2.7	38	34	75	307
		Furo Café	0.39	93.4	5658	207	705	11.4	117	52	293	1539
(III) Lagoon of the Central peninsula	(0-10)	Dwarf *Avicennia* (east side)	0.69	14.6	2338	150	63	8.1	112	20	193	268
		Dwarf *Avicennia* (west side)	0.84	63.8	2100	136	135	14.2	131	47	250	1261
		Eleocharis mutata (east side)	0.97	30.3	1000	79	41	14.1	132	20	228	689
	(40-50)	Dwarf *Avicennia* (east side)	1.30	46.4	442	43	56	14.6	146	22	276	1043
		Dwarf *Avicennia* (west side)	1.06	66.3	1108	100	97	16.4	156	39	297	1490
		Eleocharis mutata (east side)	1.03	37.5	592	50	45	12.2	134	19	232	814
(IV) *Avicennia* forest of the upper furo do Pará	(0.10)	Standing forest (south-east side)	0.77	51.3	1825	136	51	20.6	125	32	258	932
		Dead trees area (north-west side)	1.07	33.6	1050	93	44	17.1	136	22	321	979
	(40-50)	Standing forest (south-east side)	0.87	58.9	958	93	53	23.9	151	43	340	1447
		Dead trees area (north-west side)	0.74	99.4	1767	129	399	11.1	145	34	372	2193
(V) Acarajó forest upper Caeté river	(0-10)	*Rhizophora*	0.78	9.8	2783	118	161	7.1	49	17	106	92
		Avicennia	0.98	4.1	2717	114	101	7.9	43	15	88	49
		Rice field	0.96	3.9	2242	107	73	8.2	50	15	100	46
	(40-50)	*Rhizophora*	0.89	27.0	2458	100	304	12.2	75	25	165	507
		Avicennia	0.76	27.5	3342	143	614	9.7	81	30	188	609
		Rice field	1.37	2.0	1650	64	343	2.8	28	12	52	37

Significant correlations (r_{min} = 0.83): Bulk Density vs N (-0.92); Specific Conductance vs Ca (0.85), Mg (0.83), Na (0.96); P vs K (0.88), Mg (0.87); K vs N (0.85), Mg (0.97), Na (0.85); Mg vs Na (0.92).

Table 2: Dimensional characterization of mature leaves (average ± standard deviation). In a row numbers followed by the same letter are not statistically different at p = 0.05 (Fisher's Protected Least Significant Difference), n = 30 leaves per species per site except *R. mangle* in site II where n = 60.

Sites	**I**	**II**	**III**	**IV**	**V**
Leaf Dry Weight (g)					
Rhizophora mangle	0.563(0.116)a	0.584(0.141)a		0.521(0.130)a	0.609(0.192)b
Laguncularia racemosa	0.506(0.111)a, c	0.371(0.103)b		0.438(0.174)b, c	0.732(0.203)d
Avicennia germinans	0.371(0.070)a	0.468(0.285)b	0.236(0.045)c	0.433(0.130)a, b, d	0.367(0.163)a, d
Leaf Area (cm^2)					
Rhizophora mangle	37.2(6.4)a, b	39.8(8.4)a		34.4(5.6)b	46.4(15.1)c
Laguncularia racemosa	34.0(6.1)a	28.1(7.2)b		33.3(11.9)a	48.6(11.4)c
Avicennia germinans	31.0(6.0)a, b	30.4(10.8)b	17.9(2.8)c	44.7(12.1)d	35.3(13.4)a
Specific Leaf Area (cm^2/g)					
Rhizophora mangle	66.7(6.2)a	69.4(10.7)a, b		68.8(16.2)a, c	76.3(8.2)c
Laguncularia racemosa	68.1(8.0)a	76.3(5.0)b		77.1(5.7)b	67.9(9.4)a
Avicennia germinans	85.8(18.8)a	73.9(17.3)b	77.5(14.0)b	107.6(31.6)c	102.2(22.2)c
Length/Width					
Rhizophora mangle	2.4(0.3)a	2.2(0.3)b, c		2.4(0.2)a	2.3(0.1)a, c
Laguncularia racemosa	1.8(0.2)a	2.1(0.4)b		1.7(0.2)a, d	1.6(0.3)d
Avicennia germinans	2.9(0.2)a	3.4(0.7)b	2.0(0.2)c	2.5(0.3)d	2.7(0.3)e

Table 3: Average concentrations of C, S and N of mangrove leaves along the Bragança-Ajuruteua transect. Composite sample of 30 leaves (3 trees, 10 leaves per tree) (Rhi = *Rhizophora*; Lag = *Laguncularia*; Avi = *Avicennia*).

	C mol/kg			S mol/kg			N mol/kg		
Site	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**
I: Ajuruteua	41.87	43.54	40.87	0.13	0.10	0.14	1.22	1.09	1.90
II: Furos Lower Caeté	44.38	42.50	43.00	0.14	0.15	0.25	1.15	1.34	1.60
III: Central Lagoon	-	-	42.84	-	-	0.18	-	-	1.68
IV: Avicennia forest	42.32	41.21	40.30	0.16	0.13	0.11	1.46	1.22	2.36
V: Acarajó	44.35	41.50	40.68	0.08	0.10	0.15	1.36	0.98	1.90
Averages	43.23	42.19	41.34	0.13	0.12	0.17	1.30	1.13	1.89
Fisher's LSD $p \leq 0.05$	b	a, b	a		n.s.		a	a	b

	% Ash			C/N			N/S		
Site	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**
I: Ajuruteua	10.68	6.32	12.35	34	40	21	10	11	13
II: Furos Lower Caeté	8.61	7.96	9.71	39	32	27	8	9	6
III: Central Lagoon	-	-	11.11	-	-	25	-	-	9
IV: Avicennia forest	10.02	8.93	12.76	29	34	17	9	9	22
V: Acarajó	7.63	10.81	10.52	33	47	21	17	9	12
Average	9.23	8.50	11.29	34	38	22	11	9	13
Fisher's LSD $p \leq 0.05$	a, b	a	b	a	a	b		n.s.	

Table 4: Concentration of P and cations in mangroves leaves of the Bragança-Ajuruteua transect. Composite sample of 30 leaves (3 trees, 10 leaves per tree).

	P mmol/kg			K mmol/kg			Ca mmol/kg			Mg mmol/kg			Na mmol/kg		
Denomination	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**
I: Ajuruteua	31	53	46	166	166	221	153	132	30	163	168	143	745	265	960
II: Furos Lower Caeté	29	50	33	153	210	134	177	159	74	147	137	316	534	287	619
III: Central Lagoons	-	-	41	-	-	185	-	-	64	-	-	261	-	-	882
IV: Avicennia forest	34	50	48	145	271	155	162	154	50	181	163	161	743	364	1083
V: Acarajó	31	34	56	108	160	212	178	232	69	166	185	271	516	636	767
Averages	31	47	45	143	202	181	168	169	57	164	163	230	635	388	862
Fisher's LSD $p \leq 0.05$	a	b	b		n.s.		a	a	b		n.s.		a	a	b

	Fe mmol/kg			Mn mmol/kg			Na/kg			Mg/Ca		
Denomination	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**	**Rhi**	**Lag**	**Avi**
I: Ajuruteua	0.80	11.12	1.47	3.47	0.39	0.69	4.5	2.0	31.8	1.1	1.3	4.7
II: Furos Lower Caeté	0.84	8.80	1.55	5.72	1.57	3.31	3.0	1.8	8.4	0.8	0.9	4.3
III: Central Lagoons	-	-	1.41	-	-	0.52	-	-	13.7	-	-	4.1
IV: Avicennia forest	1.23	8.42	1.38	8.56	1.55	1.44	4.6	2.4	21.8	1.1	1.1	3.2
V: Acarajó	0.76	25.61	3.15	5.04	1.49	1.89	2.9	2.7	11.2	0.9	0.8	3.9
Averages	0.91	13.49	1.79	5.70	1.25	1.57	3.7	2.2	17.4	1.0	1.0	4.0
Fisher's LSD $p \leq 0.05$	a	b	a	a	b	b	a	a	b	a	a	b

Table 5: Natural abundance of ^{13}C and ^{15}N in mature mangrove leaves along the transect Bragança-Ajuruteua.
Composite sample of 30 leaves (3 trees, 10 leaves per tree) (kindly measured by Dr. L. Martinelli, CENA, Piracicaba, SP).

	$\delta\ ^{13}C$			$\delta\ ^{15}N$		
Site Name	***Rhizophora***	***Laguncularia***	***Avicennia***	***Rhizophora***	***Laguncularia***	***Avicennia***
I: Ajuruteua	-27.52	-28.98	-28.78	3.95	4.98	4.68
II: Furos Lower Caeté	-28.48	-29.20	-28.64	4.40	4.35	6.10
III: Central Lagoon			-27.01			4.95
IV: Avicennia forest	-27.54	-28.65	-29.22	5.22	8.43	6.55
V: Acarajó	-29.48	-29.25	-28.98	3.81	3.70	4.26
Average	-28.26	-29.02	-28.53	4.35	5.37	5.31
Element Concentration mmol/kg ash free dry weight	47.6	46.1	46.6	1.4	1.2	2.1